

XXIV. *On the sexes of larvæ emerging from the successively laid eggs of Smerinthus populi.* By EDWARD B. POULTON, M.A., F.R.S., F.L.S., &c., Hope Professor of Zoology in the University of Oxford.

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My friend and former pupil, Mr. R. C. L. Perkins, once told me that he had sometimes noticed that a pair of *Sphinx* larvæ found in the same stage of growth, in close proximity upon the same tree, and presumably hatched from a pair of eggs laid by the same parent, produce moths of different sexes. He inferred that this arrangement facilitated pairing, and he was led to wonder whether there is a regular alternation of sex in the successive offspring.

On the other hand, it appeared quite possible that the cases which he had observed were exceptional, and that the succession is irregular, or that it is such as to facilitate intercrossing rather than frequent pairing between closely related individuals. This latter view is suggested as a probable one by the numerous adaptations by which wide intercrossing is favoured in other departments of organic nature, and by the following direct evidence. Mr. W. Hatchett Jackson and Mr. O. H. Latter have observed that the pupæ obtained from different batches of larvæ of *Vanessa io* "were principally, but not entirely, of one or of the other sex."* It is generally admitted that the separate colonies of *Vanessa* larvæ are, at any rate as a rule, hatched from different batches of eggs. Such an observation, if confirmed, is to be interpreted by one of two suppositions. We must either suppose that the whole mass of eggs of each female *Vanessa* produces a great preponderance of one and the same sex (males in some individuals and females in others), or that different batches of eggs laid

* Trans. Linn. Soc. Lond., vol. v., 1890, p. 156.

by the same individual produce now a preponderance of one sex, and now of another. Either of these alternatives would appear strongly to favour intercrossing. The following observations, so far as they go, tend to support the latter alternative.

A pair of *Smerinthus populi* were found *in coitu* in an Oxford garden, between 10 and 11 a.m., on May 25th, 1893. They were carefully removed, and remained together until 8.40 p.m. The attempt was made to observe the order in which the eggs were laid, and to rear the larvæ separately, the sexes being determined in the pupal state. The results are most concisely shown in a tabular statement.

Date.	Number and order of eggs laid.	Sexes produced. M = male ; F = female.	Observations.
May 25.	44 eggs laid, order unnoted.	15 M 28 F	1 missing (unknown whether the egg hatched). 1 male and 1 female moth emerged in the hot summer of 1893. 1 male pupa was deformed and dead.
May 26.	47 eggs laid.	—	All these eggs, the order of which had been carefully noted, hatched during my absence from home, and the larvæ were lost.
May 27.	34 eggs laid. The order of the first 22 unnoted.	9 M 8 F	4 missing ; 1 larva died. 1 female moth emerged 1893. 1 male pupa was deformed and dead, and another rather deformed.
	23	—	Larva died small (probably 3rd stage).
	24 M	Pupa rather deformed.
	25 F	
	26 M	
	27 M	
	28 M	
	29 M	
	30 M	
	31 F	
	32 F	
	33 M	
	34 M	Moth emerged 1893.
		Total 17 M, 11 F	

Date.	Number and order of eggs laid.	Sexes produced. M = male ; F = female.	Observations.
May 28.	28 eggs laid, order shown below.		
	1 F ..	Moth emerged 1893.
	2 F	
	3 F	
	4	Larva died in 3rd or 4th stage, owing to accident to branch of food-plant.
	5 M	
	6 F	
	7 F	
	8	Larva died in 3rd or 4th stage.
	9 M	
	10 F	
	11 M	
	12 M	
	13 M	
	14 M	
	15 F	
	16 M	
	17 M	
	18 F	
	19 M	
	20 M	
	21 F	
	22 M	
	23 F	
	24 F	
	25 F	
	26 F	
	27 M	
	28 M	
		Total 13 M, 13 F	
May 29.	8 eggs laid, order unnoted.	4 M 2 F	1 missing ; 1 larva died. 1 male moth emerged 1893. 1 male pupa dead and deformed, and 1 very small and rather de- formed.
May 30.	14 eggs laid. order unnoted.	7 M 4 F	3 larvæ died.
May 31.	7 eggs laid, order unnoted.	1 M 6 F	
June 1.	3 eggs laid, order unnoted.	1 M 1 F	1 egg did not hatch.

Date.	Number and order of eggs laid.	Sexes produced. M = male ; F = female.	Observations.
June 2.	7 eggs laid, order shown below.		
	1 F	
	2 M	
	3 F	
	4 F	
	5	Larva hatched, but died very small.
	6	Did not hatch. Probably no development took place; egg blackened.
	7	Ditto. ditto.
		Total 1 M, 3 F	
June 3.	1 egg laid.	—	Larva did not hatch, but was apparently fully formed in the egg.

The total number of eggs laid on each successive day forms an interesting curve rising to a maximum on the second day and declining very rapidly on the fifth.

The most striking result shown in these tables is the remarkable change in the proportion of the sexes on different days. Thus on May 25th there were nearly twice as many females as males, on May 27th over 50 per cent. more males, while on May 28th the numbers were equal. It is possible that this change in proportion may follow some biological law, especially when considered in connection with Mr. Jackson's and Mr. Latter's above-mentioned observations. It is at any rate enough to suggest further observation. At present, however, as I learn from Mr. Francis Galton, to whom I have submitted the figures, the numbers are not large enough to warrant any such conclusion.

With regard to the succession of the sexes in a series of individuals (May 27th, 28th, and June 2nd), the arrangement does not appear to differ from that of black and white balls drawn successively out of a bag containing equal numbers of each. But here, too, wider observations are required. The arrangement in little groups of the same sex *may* possibly be adapted to favour cross-fertilisation. But even in drawing pairs of

black and white balls, two of the same colour will be drawn together twice as frequently as those of different colours. In future observations of a sluggish species like *Smerinthus populi*, it would be desirable to track the moth as it lays little groups of eggs on different leaves, and to rear such groups separately. We must not altogether put aside the remote possibility that the parent may possess some power of controlling the sex of her offspring.

Six moths emerged in the hot summer of 1893; three of these were males and three females. The eggs from which these individuals were hatched were scattered through the successional series, and were not peculiar to any part of it, and the same appears to be true of the deaths of larvæ and deformity of pupæ.

Failures to hatch, however, are confined to the end of the series, unless some of the "missing" larvæ are to be explained in this way. This tendency is especially clearly seen on the last two days, and yet the very last egg laid contained a well-formed larva which was unable to hatch.

Even the small number of larval deaths which took place are chiefly to be accounted for by the conditions of the experiment. Thus, considering only the eggs laid during May (and omitting the later eggs because of the frequent failure to hatch), we find out of 40 larvæ reared in separate sleeves (23 to 34 on May 27th, and the 28 on May 28th) only two deaths occurred, not including the manifestly accidental death of the fourth larva on May 28th. On the other hand, out of 95 larvæ reared in groups of from 3 to 8 (usually 7) in number, 11 larvæ died or were missing. From this it may be inferred that larvæ are in some way injured by being reared in groups with a much greater relative proximity than in nature. I have also found this to be true of *S. ocellatus*; for, when groups of more than 10 or 12 small larvæ were enclosed in sleeves of moderate size, it was always found that the numbers became reduced to a maximum of about a dozen, and often much lower; whereas groups of smaller numbers were frequently maintained without any deaths.

The list as a whole strongly impresses upon us the comparative rarity of death from internal causes (including disease), and the overwhelming importance of

the struggle with highly organised enemies in determining the vast amount of destruction which occurs among these animals in the natural state.

The unfortunate loss of the 47 larvæ of May 26th served to show that the period of development within the egg is extremely uniform. The eggs laid on May 25th had been properly enclosed, and I thought I was safe in leaving the others for a day. On my return every one of the eggs laid on the 26th had hatched, and the larvæ had escaped; while not a single larva had emerged from any egg laid at a later date.

Six of the male pupæ were deformed, but not one of the females.

The total number of eggs laid was 193, and subsequent dissection revealed a single egg in the body of the parent moth. From these eggs 68 female and 59 male pupæ were obtained.

The results afford no support to the opinion that the sex of insects can be determined by external conditions during larval life. With conditions of very complete uniformity, the proportions of the sexes—68 females to 59 males—appear to be normal. It may be admitted that the larger female larvæ require more food, chiefly to prepare for the amount of material to be stored up in the ova. It would not therefore be at all surprising if the female larvæ were starved before the males when a minimum of food was supplied. The consequent emergence of a number of males would in no way support the view that a scanty diet “determines” this sex. It is probable that some writers on this subject have mistaken *favouring* for *determining* conditions.

There was no tendency towards the predominance of males in the last-laid eggs, and therefore no indication that this sex may be determined by exhaustion (in itself most improbable) of the spermatozoa.